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Modelling reproductive strategies of *Daphnia*

Das Modellieren der Vermehrungsstrategien von *Daphnia*

By Wilfried Gabriel

With 2 figures and 1 table in the text

Abstract

A model is developed which predicts growth and reproduction of *Daphnia* without any growth function. Inputs to the model are net production rates depending on body weight and measured or assumed mortality rates. Partition of energy into growth and reproduction are determined by the postulate that the adaptation to environmental conditions including mortality maximizes the probable total reproduction. Good quantitative and qualitative agreement with experimental data on *Daphnia pulicaria* is obtained with the assumption of a moderate size dependent mortality.

Introduction

Parthenogenetically reproducing daphnids are usually considered to be opportunistic and "r selected" (Allan, 1976), although there may be gradual differences in the manifestation of this character, especially when food is limited (Hrbáček, 1977). Therefore, they should be selected for a maximum number of offspring under the given environmental conditions.

Daphnia species grow further after reaching maturity. Under identical food conditions large specimens carry more eggs than smaller ones (Green, 1954). On the other hand larger animals suffer from increased natural mortality (Allan, 1976; Lynch, 1980) and vertebrate predation (Zaret, 1980). As the amount of energy which can be utilized by an animal is limited by the availability of food and its harvesting capabilities, an optimization problem arises. The daphnid has to share the available energy in somatic growth and reproduction as to maximize the output of young. If there were no increased mortality for large individuals it would make sense to postpone maturity and to put all the net production into somatic growth first, thus growing to a large size and then having large numbers of eggs. At the other extreme, with high mortality rates, it would be more efficient to put all the available energy into reproduction as early as possible, mature early, and stay small. Clutch size would be smaller in this case, but the total number of offspring could be increased, because the life time of the mother is longer. These two life history tactics have in fact been found in fishless and fish-inhabited water bodies respectively (Hrbáček & Hrbáčkova-Isslová, 1960; Stenson, 1972). They form part of the arguments supporting the "Size Efficiency Hypothesis" (Hall et al., 1976).

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Partition of net production between body growth and reproduction is, therefore, one of the key processes which determine the life history of an animal. I present here a simple mathematical model, which is based on the assumption that this process is optimized to gain a maximum number of young for given conditions of food availability and mortality. The model predicts the time course of growth and reproduction of a daphnid only from basic measurable metabolic parameters as assimilation and respiration, and from assumed mortalities.

Outline of the model

The net production can be measured as the differences between assimilation and respiration for instance, provided the losses as excreta and exuviae are small enough to be neglected (WINBERG, 1971). These rates are influenced by body weight and environmental factors like temperature and food concentrations. I assume that the partition of the net production into growth and reproduction will follow an optimal function which maximizes the reproduction weighed with the probability of survival and summed over the total lifespan. There may exist a lot of mathematical functions which can describe the behaviour in question, but the specific analytic expression is of little interest as long as the biological relation is well reproduced. For that reason we can take any function, e. g. a polynomial of high order, if this function has sufficient variability to describe all possible reproductive tactics. The coefficients of such a polynomial, however, or the parameter of other functions are stringently determined by the postulate of maximum total reproduction. Therefore, finding this maximum gives all necessary information for the prediction of growth and reproduction and there are not parameters left for "tuning" the model.

Mathematical Formulation of the Model

As a first step one has to know the dependence of the net production rate dP/dt on the body weight W.

$$\frac{dP}{dt} = f(W); \tag{1}$$

one can use e.g.

$$\frac{dP}{dt} = a_1 W^{b_1} - a_2 W^{b_2} \tag{1a}$$

where

P = net production;
W = body weight;
a_1, b_1 = assimilation coefficients;
a_2, b_2 = respiration coefficients.

The equation (1 a) is based on the anabolism-catabolism concept of BERTAANFFY (1941, 1964) and expresses the net production rate as the difference between assimilation rate and respiration rate. It has to be carefully checked for which range of W this expression is valid, because the coefficients, especially a_1 and a_2, are in general not independent of W. Instead of (1 a) one may use any other relation, for instance a direct parametrisation of measured data of net production.

Knowing the net production rate (1) we can write the growth rate

$$\frac{dW}{dt} = \frac{dP}{dt} \cdot (1 - \alpha\,(W,\vec{x})) \tag{2}$$

where

α = function which calculates the portion of net production put into reproduction ($0 \leqq \alpha \leqq 1$);

$\vec{x}$ = $(x_1, \ldots, x_n)$ is a parametrisation vector, which gives the dependence of this portion on the actual body weight.

As long as the function α can describe the behaviour in nature, the results of this model are not influenced by the functional expression used for α. I chose the following polynomial

$$\alpha(W,\vec{x}) = \sum_{i=1}^{n} x_i \left(\frac{\frac{dP}{dt}}{W}\right)^{i-1} \tag{3}$$

because the dependence of α on the relative production rate seems to be quite linear so that $n = 5$ already gives a satisfactory degree of freedom for most cases.

From the growth rate equation (2) it follows for the reproduction rate dR/dt

$$\frac{dR}{dt} = \frac{dP}{dt} \cdot \alpha(W,\vec{x}) \tag{4}$$

Integrating the system of the two differential equations (1) and (2) with a computer by usual methods of numerical mathematics we can calculate the reproduction for a certain time interval. If we assume a non zero mortality rate, we have to multiply the reproduction rate with the probability of survival s. The probable reproduction R_{prob} in the time interval Δt is then

$$R_{prob} = \int_{\Delta t} \frac{dP}{dt} \cdot \alpha(W,\vec{x}) \cdot s(W,t)dt \tag{5}$$

The probability of survival is easily related to the often used daily mortality rate by

$$s(W,t) = (1 - m(W))^t \tag{6}$$

where

$m(W)$ = daily mortality rate at body weight W and

t = time measured in days.

The optimization problem is now to find in maximum of R_{prob} with Δt equal to the life-span; that is, we have to find the functional dependence of α on W which maximizes the integral in (5). In other words we have to find the maximum of the function R_{prob} with respect to the vector $\vec{x}$. This can be calculated by numerical mathematical methods, as given e.g. by FLETCHER & POWELL (1963) or FLETCHER & REEVES (1964).

As the output of the maximization we get the vector $\vec{x}$, for which $\alpha(W, \vec{x})$ follows the optimal reproductive tactic for each body weight.

With this knowledge one can integrate the equations (1) and (2) again and now predict the whole life-pattern of growth and reproduction.

Test of the model with experimental data

The applicability of the model has been tested by the following comparison of the predictions with the data of a longterm experiment carried out by LAMPERT (1977). Coefficients of the BERTALANFFY equation and length-weight-relationships at two food concentrations taken from this study serve as input to the model. The net production outside the range of the experiment is estimated by extrapolation. Input parameters are listed in Table 1. It is unknown to which mortality rate the animals were best adapted. Therefore,

Table 1. Input parameters of the model.

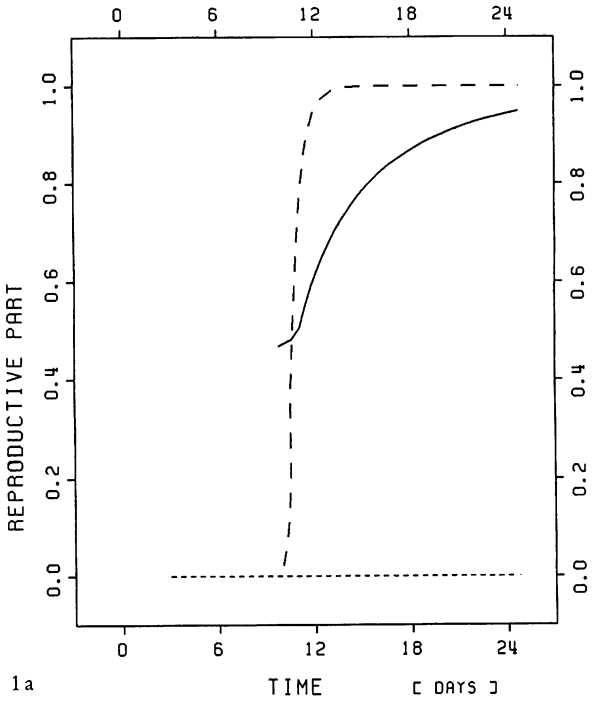
Parameter		Food concentration (*Scenedesmus*) low (0.1 mg C/l)	high (1.0 mg C/l)
Time period of the optimisation (life span) in days		50	50
Starting weight (carbon content in μgC)		3	3
Minimal weight upon reaching maturity (carbon content in μgC)		15	15
Relation between length L (in mm) and weight W (carbon content in μgC)			
$L = aW^b$	a	3.0	4.9
	b	2.65	2.59
Bertalanffy coefficients	a_1	0.021	0.041
	b_1	0.91	0.83
	a_2	0.0094	0.01
	b_2	0.88	0.75
Assumed daily mortality rates			
zero-mortality		0	0
size independent		0.1	0.24
size dependent		$0.005 \cdot L^2$	$0.005 \cdot L^2$

several mortality rates have been studied: zero-mortality, size independent and size dependent mortality. Some results are shown together with the experimental data in the Fig. 1 a—d for low food concentration and in the Fig. 2 a—d for high food concentration. The experimental data are represented by open dots, the results of the model are drawn by lines: shorter dashes for zero-mortality, longer dashes for size independent mortality and solid lines for size dependent mortality.

For zero-mortality the reproductive part α (Fig. 1 a, 2 a) of the net production is zero for the time period, where experimental data are available. For that reason the reproduction (Fig. 1 b, 2 b) starts very late (and out of the time scale of the figures). As the net production is used only for somatic growth, the predicted body weight (Fig. 1 c, 2 c) increases after reaching maturity much faster than in the experiment. As long as the reproduction rate is zero there is no difference between body weight and net production and the net production (Fig. 1 d, 2 d) has maximal possible values at any time, because net production increases with body weight and no slow-down of the growth occurs by reproduction.

The model needs a non-zero mortality to begin with reproduction as early as seen in the experiment. But with a constant mortality rate (long dashes in the figures) for the whole life until natural death the function α changes in too short a time period from minimum value 0 to the maximum value 1, so that the curve of body weight follows the zero-mortality line for some time and then suddenly deflects to a line of constant body weight. The net production rate remains constant for fixed body weight and for that reason the reproduction and net production follow a straight line after α reaches 1. If one runs the model with a lower or higher constant mortality the reproduction starts later respectively earlier but the qualitative behaviour does not change. Besides these discrepancies between data and model one has to choose different constant mortality rates for high and low food concentration in order to get at least some points close to the experiment.

To describe the experiment by the model one has to assume the animals to be adapted to a more complex structure of mortality. The results become realistic with the simple hypothesis that mortality is increasing with visibility. The solid lines in the figures are the model predictions for size dependent mortality using the same function $m = 0.005\,L^2$ (with L = length in mm and m = daily mortality rate) for both food concentrations. To evaluate the agreement with the experiments one should take into consideration that all curves are totally determined by the input parameters and that no further adjustments to the data are possible: With the assumed mortality and with the measured metabolic parameters the reproductive and the somatic parts of the net production are calculated by the optimization procedure for each body weight. Therefore, the time course of production, growth and reproduction are fixed


0
6
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18
24
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0.4
0.6
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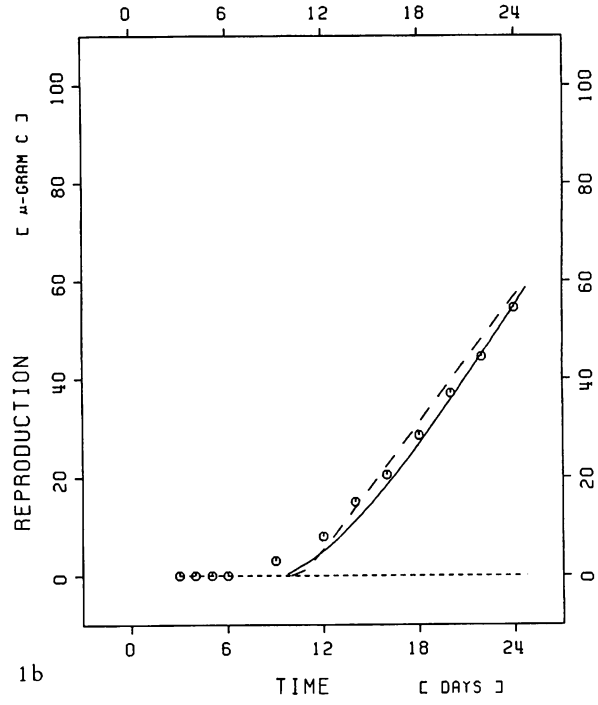
REPRODUCTIVE PART
TIME
[DAYS]

1a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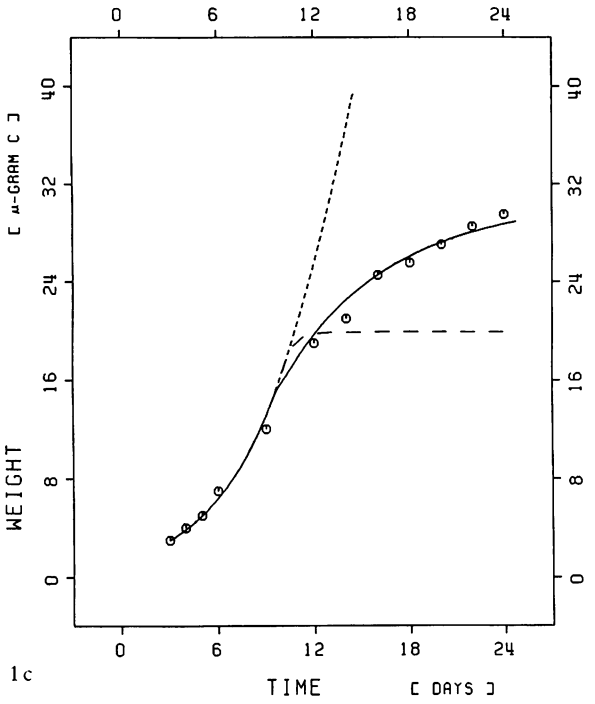
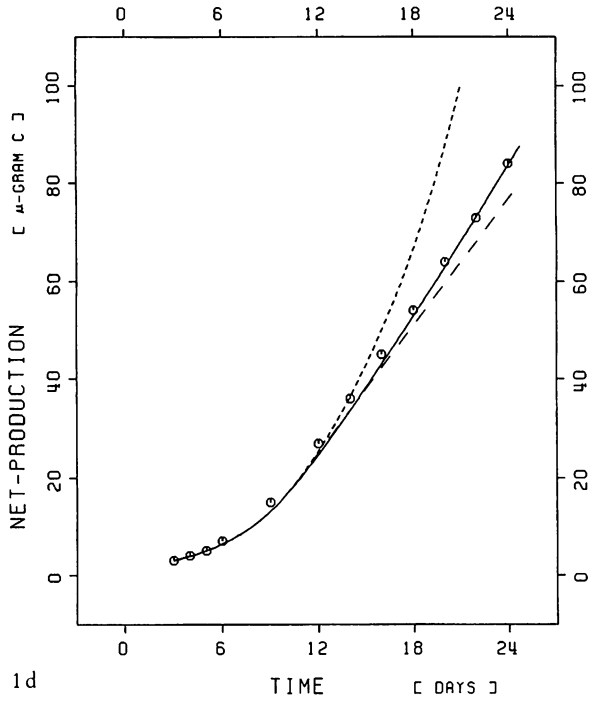
1b

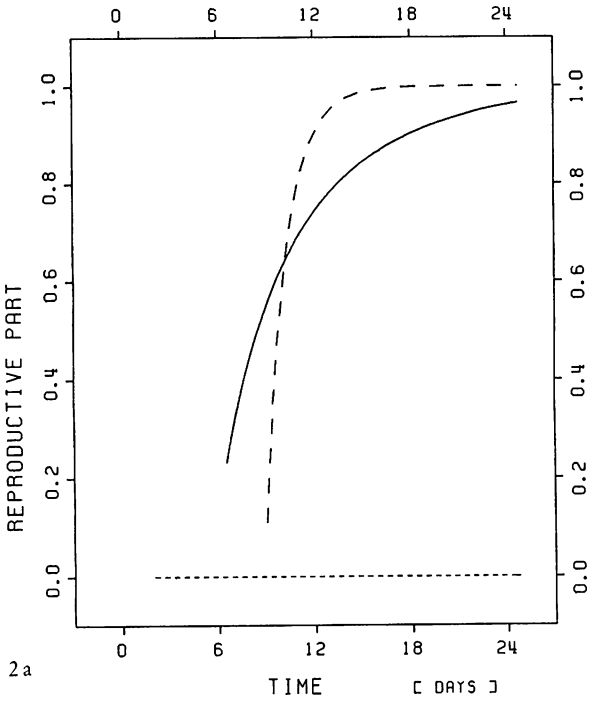


1c



1d

Fig. 1 a—d. Time courses of (a) reproductive part α of the net production, (b) reproduction, (c) body weight, and (d) net production. Open dots are experimental data. Lines are model predictions: shorts dashes with zero-mortality, long dashes with size independent mortality, and solid lines size dependent mortality. The food concentration is low.


REPRODUCTIVE PART
0.0
0.2
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1.0
0
6
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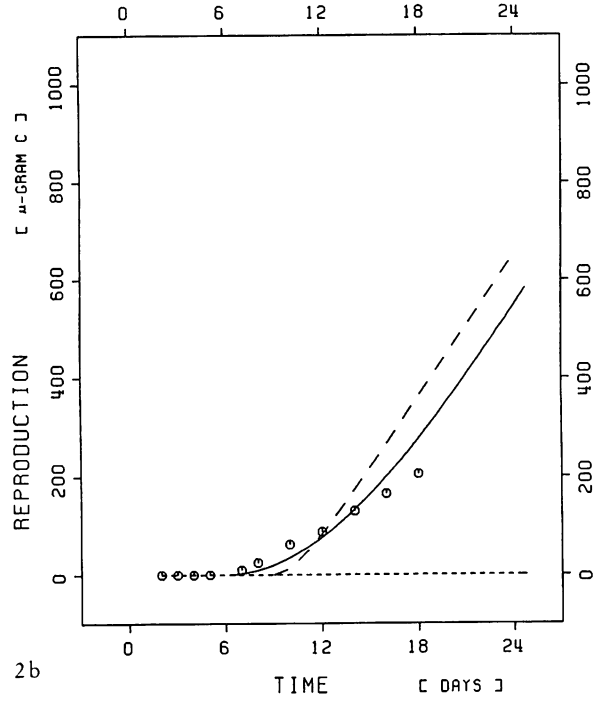
18
24
TIME
[DAYS]

2a


REPRODUCTION
[µ-GRAM C]
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400
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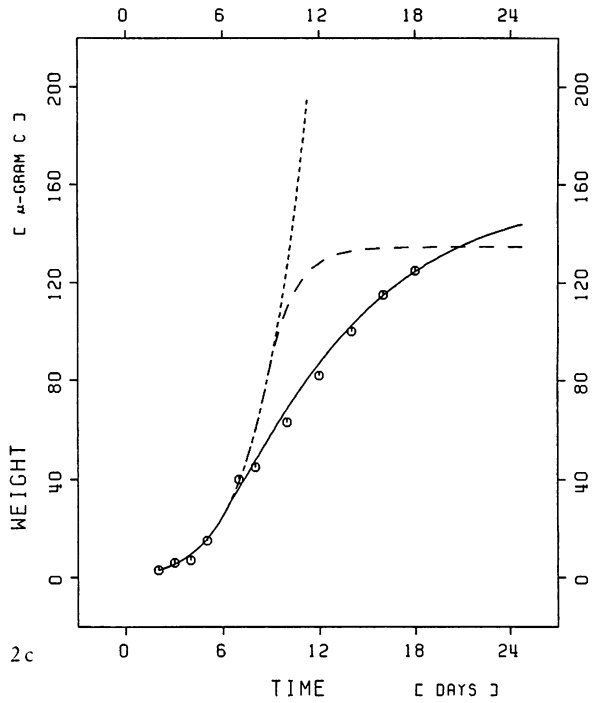
1000
0
6
12
18
24
TIME
[DAYS]

2b



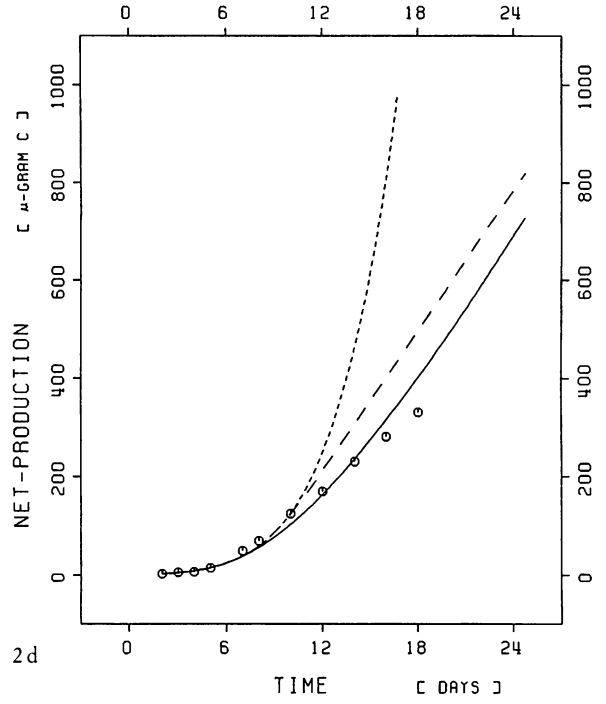


Fig. 2a—d. Same as figures 1a—d, but for high food concentration.

by the starting point, so that a small change at any time and especially at the beginning may cause a dramatic change after a short time period.

Discussion

The model presented predicts growth and reproduction of *Daphnia* without any growth function. It has to be pointed out that the growth curve of the animal is a result of the optimization process. Realistic results for *D. pulicaria* are only obtained, when a size dependent moderate mortality is assumed. The model, therefore, predicts *D. pulicaria* to be best adapted to moderate vertebrate predation. In Europe this species is known to live in large fish ponds, where it can persist at moderate levels of fish predation, but disappears at high predation pressure (FOTT et al., 1981).

Although a good qualitative and quantitative consistency with experimental data has been shown, I propose further crucial experimental tests for the model. Only two concentrations of food could be tested because of the lack of data from long-term experiments. Thus by studying additional food concentrations one should confirm that the agreement is not accidental. Moreover, the experimental conditions should be altered during the course of an experiment and the results compared to the predictions of the model.

Then the model should be applied to *Cladocera* other than *D. pulicaria*, which live in different habitats. Metabolic input data have to be determined experimentally for this purpose.

Besides this the model could help to explain the shift to smaller sizes at first reproduction often observed in populations of cladocerans in the field (LYNCH, 1979; BRAMBILLA, 1980). Information on mortality rates must be available in this case.

It is easy to understand that natural selection acts to maximize the reproductive rate in a variable environment. Thus the basic assumption of this model seems to be realistic. It is, however, limited to "r selected" species and cannot be valid for "K selected" ones. Reproductive success is certainly one important factor determining the fitness of a population, but there are more factors involved. Selective mortality of small stages, e.g. by invertebrate predators, is one of these parameters. It probably has to become incorporated to sufficiently describe the life history tactics of species other than *Daphnia pulicaria*.

Zusammenfassung

Es wird ein Modell für Wachstum und Reproduktion von Daphnien ohne Benutzung irgendwelcher Wachstumsfunktionen entwickelt. Eingabeparameter für das Modell sind die experimentell bestimmbare, gewichtsabhängige Nettoproduktionsrate und eine angenommene oder gemessene Mortalität. Das Modell optimiert die Aufspal-

tung der Energie in somatisches Wachstum und Eiproduktion unter der Annahme, daß Daphnien daran adaptiert sind, im Laufe ihres Lebens die Zahl ihrer Nachkommen zu maximieren. Dadurch wird der gesamte zeitliche Ablauf von Wachstum und Reproduktion vorhergesagt. Das Modell kann die verfügbaren Daten eines Langzeitexperiments mit *Daphnia pulicaria* bei niedrigen (Fig. 1 a—d) und hohen (Fig. 2 a—d) Futterkonzentrationen gut reproduzieren, wenn man in Übereinstimmung mit Freilanduntersuchungen eine geringe, längenabhängige Mortalität annimmt.

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References

Allan, J. D. (1976): Life history patterns in zooplankton. — Am. Natural. **110:** 165—180.

Bertalanffy, L. v. (1941): Stoffwechseltypen und Wachstumstypen. — Biol. Zbl. **61:** 510—532.

— (1964): Basic concepts in quantitative biology of metabolism. — Helgoländer wiss. Meeresunters. **9:** 5—37.

Brambilla, D. J. (1980): Seasonal changes in size at maturity in small pond *Daphnia*. — In: W. C. Kerfoot (ed.): Evolution and ecology of zooplankton communities. — Amer. Soc. Limnol. Oceanogr. Spec. Symp. **3:** 438—455.

Fletcher, R. & Powell, H. J. B. (1963): A rapid descent method for minimization. — Computer Journal **6,** 2: 163—168.

Fletcher, R. & Reeves, C. M. (1964): Function minimization by conjugate gradients. — Computer Journal **7,** 2: 149—154.

Fott, J., Pechar, L. & Pražáková, M. (1981): Fish as a factor controlling water quality in ponds. — Developm. in Hydrobiol. **2:** 255—261.

Green, J. (1954): Size and reproduction in *Daphnia magna* (Crustacea: Cladocera). — Proc. zool. Soc. Lond. **124:** 535—545.

Hall, D. J., Threlkeld, S. T., Burns, C. W. & Crowley, P. H. (1976): The size-efficiency hypothesis and the size structure of zooplankton communities. — Ann. Rev. Ecol. Syst. **7:** 177—208.

Hrbáček, J. (1977): Competition and predation in relation to species composition of freshwater zooplankton, mainly Cladocera. — In: Cairns, J., jr. (ed.): Aquatic microbial communities, Garlands Publishing, New York: 305—353.

Hrbáček, J. & Hrbáčková-Esslová, M. (1960): Fish stock as a protective agent in the occurrence of slow-developing dwarf species and strains of the genus *Daphnia*. — Int. Rev. ges. Hydrobiol. **45,** 3: 355—358.

Lampert, W. (1977): Studies on the carbon balance of *Daphnia pulex* as related to environmental conditions. I., II., III. — Arch. Hydrobiol. Suppl. **48** (314): 287—360.

Lynch, M. (1977): Fitness and optimal body size in zooplankton populations. — Ecology **58:** 763—774.

— (1979): Predation, competition, and zooplankton community structure: An experimental study. — Limnol. Oceanogr. **24:** 253—272.

— (1980): The evolution of cladoceran life histories. — Quart. Rev. Biol. **55:** 23—42.

Stenson, J. A. E. (1972): Fish predation effects on the species composition of the zooplankton community in eight small forest lakes. — Institute of Freshwater Research, Drottningholm, Sweden, Report No. **52:** 132—148.

Winberg, G. G. (1971): Methods for the estimation of production of aquatic animals. — Academic Press, London and New York.

Zaret, T. M. (1980): Predation and freshwater communities. — New Haven, London, Yale Univ. Press.

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